

**To defend or to Not defend? To study resource dependent territoriality in
a Sunbird community in Anaikatti hills, Western Ghats**

By

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Under the Supervision of

Dr. Bilal Habib

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**भारतीय वन्यजीव संस्थान
Wildlife Institute of India**



DECLARATION

I hereby declare that the work conducted under the thesis entitled “**To defend or to Not defend? To study resource dependent territoriality in a Sunbird community in Anaikatti hills, Western Ghats**”, is a record of original and independent research work done by me and subsequently submitted for the award of the degree of **Master’s in Wildlife Science** at the **Academy of Scientific and Innovative Research**. This research work has been carried out under the guidance and supervision of **Dr. Bilal Habib, Scientist- F**, and co-supervision of **Dr. Rajah Jayapal, Senior Principal Scientist** of Wildlife Institute of India, Dehradun. The work has not formed the basis for the award of any other degree, diploma, or any other qualification. I also declare that the thesis embodies my own work, analysis, observation, understanding and the particulars given in it are true to the best of my knowledge.

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CERTIFICATE

This is to certify that the thesis by **Sneha Rethinam Sakthivel** entitled “**To defend or to Not defend? To study resource dependent territoriality in a Sunbird community in Anaikatti hills, Western Ghats**” is an original and independent research work submitted to the **Academy of Scientific and Innovative Research**, for the award of the degree of **Master’s in Wildlife Science**.

Sneha Rethinam Sakthivel has put one semester of research work embodied in this thesis under my guidance and supervision. The work presented in this thesis has not been submitted to any other University or Institute for the award of any degree, diploma or distinction.

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I have postponed and procrastinated as much as I could to write this chapter of my thesis, for I know, writing this means I have to come face to face with the fact that, WII is ending. Not because I'm fond of the memories I made in WII but because the past two years have been a roller coaster ride of emotions, of relationships, of events that I'm still trying to comprehend. Writing this chapter means I have to deal with all of that, probably why I waited till the very last minute to write it. Or Maybe I was meant to write it here, in the deafening confluence of Alaknanda and Laxman Ganga drowning the weight of my memories.

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1. Summary

Sunbirds are excellent model organisms to study resource dependent territoriality or feeding territoriality due to their dependence on nectar which is both renewable as well as quantifiable. It is well established in many of its ecological counterparts such as American hummingbirds of family Trochilidae, Australian honeyeaters of family Meliphagidae, and Hawaiian honeycreepers of the family Fringillidae. This study is exploratory research aimed to find the presence of feeding territoriality in an Indian sunbird community as well as to test the threshold model of feeding territoriality. The study was done in an heterogenous resource landscape which is not quite comparable to previous studies done on acres of land dominated by single plant species. Though the sunbird community agreed to some basic principles, the results reflect a much complex response to changes in flower abundance and intruder pressure.

2. Introduction

The vast majority of knowledge that we have of bird behaviour are based on research on temperate birds. Tropical birds are hugely under-represented, giving rise to a temperate zone bias. Temperate bird behaviour has traditionally been considered typical of birds, and those of tropical, a deviation from the “normal”. We understand that, a knowledge gap exists in understanding the behavioural ecology of tropical birds at large (Eugene S. Morton, 2000). Tropical birds are fascinating. Their ecology has more biotic determinants than their temperate counterparts, whose behaviour vastly is influenced by the strong abiotic stimulus like temperature and photoperiod.

The case of Territoriality of birds also faces a similar issue. We still widely use a temperate based model, that males establish and defend breeding territories during the breeding season (Freed, 1987). Their territoriality is triggered due to an increase in blood testosterone levels which is a response to increasing photoperiod in spring (Wingfield et al., 1990). However, tropical birds that breed throughout the year, like Sunbirds, of the family Nectariniidae, exhibit territoriality all through the year. An even more interesting aspect is that of feeding territoriality that is well established in golden winged sunbirds and other African sunbirds (Earlé, 1982; Evans, 1996; Frost & Frost, 1980; Gill & Wolf, 1975; Pyke, 1979). These papers suggest that sunbirds are capable of altering their territorial behaviour depending on the resource abundance and intruder pressure. Feeding territoriality can be considered a form of facultative territoriality.

“**Facultative territoriality**” implies that territoriality is not a mandated behaviour, but an adaptive strategy that occurs when the net benefits are positive (Lederer, 1981). And it is possible to defend resources without holding territories (Carpenter and MacMillen, 1976). Nectar-producing flowers are often defensible in terms of their physical characteristics because they provide a site-specific renewable resource (Wolf and Hainsworth 1971).

Though the breeding behaviour of Indian sunbirds are fairly well studied, the nature of territorial behaviour especially that of feeding territoriality is still quite disputed (Lamba, B.S, 1978; Prabhat Kumar, 2014; Wesley, 2004). It is a widely held belief by many ornithologists, that sunbirds are very aggressive. At the same time, anecdotal records of sunbird aggregations on densely flowering plants are also not uncommon. One of the aims of the study was to probe into this existing discrepancy and to test the threshold model of feeding territoriality.

Threshold model of territoriality suggest that territoriality is beneficial only along a narrow range of resource abundance and competitor/intruder pressure. The model predicts that in nectarivorous birds, the territorial behaviour occurs above a lower threshold of nectar productivity and disappear above an upper threshold (Carpenter & MacMillen, 1976). The number of flowers determined the occurrence of feeding territoriality in golden winged sunbirds in Africa (Gill & Wolf, 1975). These studies also explored the economics of feeding territoriality in terms of energetics by calculating the net energy gains from a foraging area of a territorial bird vs a non-territorial bird and comparing it with cost of living as a territorial bird vs the cost of living as a non-territorial bird.

The honeycreepers were found to be non-territorial (measured by cost of living per bird) at both low and high flower abundances, but they were found to be intensely or moderately territorial at intermediate flower abundances. In Australian new holland honeyeaters, territory exclusiveness, measured as proportion of intruders expelled, was highest only at moderate nectar levels and lower when nectar was very poor or very high (McFarland, 1996). They responded to intruders by reducing territorial behaviour with increasing visitation rate of intruders.

The objectives of this study are as follows;

1. To represent graphically the temporal dynamics of sunbird resources
2. To measure the quantity and quality of sunbird resources
3. To quantify visitation and resource defence
4. To find relationship of territorial behaviour with change in resources abundance and intruder pressure.

Under what circumstances do sunbirds become territorial or show more aggression is the aim of this study.

3. Methods

3.1 Study area

3.1.a Geographic location and physical features

The study was carried out in and around the serene campus of Salim Ali Centre for Ornithology and Natural History in Anaikatti hills, at an altitude of 600m asl. Anaikatti hills is part of the southernmost range of the central western ghats. It falls in the rain shadow region of the Nilgiri hills, a biosphere reserve and a UNESCO world heritage site. The terrain is mildly to severely undulating. It gets most of its rainfall during the north east monsoon and partly from South west monsoon (Paramasivam et al., 2015). It is a seasonally dry tropical biome. The study season (from December 2024 to April 2025), post North east monsoon saw a number of sporadic rainfalls that was quite atypical of the landscape. mild spring, fry winters

3.1.b Vegetation

The vegetation type is scrub jungle, dominated by deciduous trees like *Chloroxylon swietenia* and *Acacia sp.* and interspersed with evergreen trees like *Casine glauca* and shrubs like *Glycosmis mauritiana*, *Todalia asiatica* and *Carmona retusa*. The study area was heavily infested with *Chromolaena odorata* during the months of December to February, following the northeast monsoons, after which the herb dried up in the months of march and April. both flora and fauna typical of evergreen forests also thrive in some suitable areas.

Though sunbirds were seen feeding from many plants the only consistent and substantial flowers were that of the planted trees. *Tecoma stans* was one such exotic shrub, native to the tropical and subtropical Americas. It thrives in well-drained low to medium fertility soils and is considered an invasive in many countries (Singh et al., 2024). Some of them had naturally regenerated and were found growing inside forests. Another avenue tree, *Millingtonia hortensis* was also observed attracting sunbirds. Sunbirds are usually seen aggregating on these trees. Among these exotic trees, one native tree, *Erythrina stricta*, which flowered during the spring of 2025, also attracted many sunbird visitors among other bigger bodied birds. Many sunbird flowers bloomed during my study period, but they were either very few in number, or their nectar was too low in quantity to be measured using my instruments.

3.1.c Avifauna

The vibrant sunbird community of the dryer areas of Anaikatti hills comprise of three species; *Cinnyris asiaticus* (purple sunbird), *Cinnyris lotenius* (lotens sunbird) and *Leptocoma zeylonica* (purple rumped sunbird). In the wet evergreen areas, *Leptocoma minima* (crimson backed sunbird) is also found, though, I have not encountered any in my study area, during the study period. “Sunbirds” hereafter will refer to these **three** sunbirds unless otherwise specified.

C. asiaticus is distributed from UAE, Baluchistan, Pakistan, India Nepal, Sri Lanka, Bangladesh to Indochina and south Yunnan. *L. zeylonica* is endemic to the peninsular India south from Nasik, Jabalpur and Lohar Daga; assam and south Bengal, Bangladesh and Burma, and Sri Lanka. *C. lotenius* is endemic to south India and Sri Lanka (Robert & Mann, 2001).

3.2 Field methods

3.2.1 Quantifying resources

Identifying flowering plants

During the initial two weeks of my study period as well as regularly throughout the study, the campus and the surrounding areas (up to 2 km radius) were regularly surveyed for flowers that were foraged for nectar by sunbirds (hereafter **sunbird flowers**). The book “Flowering plants of SACON campus in the Anaikatty hills, Western Ghats” was used to determine the species identity of the plant. Sunbird flowers were surveyed by walking on forest trails, and looking for direct sighting of sunbirds foraging for nectar on flowers. It was also done by waiting near a “potential” sunbird flower and confirming. After observing the morphologies of a couple of sunbird flowers, it is intuitive to guess if a flower could be a potential nectar source for sunbirds. I do have to admit I was disappointed by many flowers and quite surprised by some too. Also, a word of caution; by sunbird flowers, it shouldn't be inferred that they are sunbird pollinated, just infer as a nectar source. To even assertively claim, a sunbird visited a flower just for nectar was a little problematic, as the sunbird may have probed the flowers for insects or spiders or even for drinking water!(Salim Ali, 1932).

Only flowers that attracted sunbirds repeatedly (visitation rate to patch > approx. 2 visits per hr) and in which they probed the corollas predictably to consume nectar were considered sunbird flowers. Though the flowering periods of all sunbird flowers were observed and noted down to understand how dynamic sunbird resources were, not all sunbird flowers were used to collect behavioural data, as some plants did not attract sunbirds consistently and predictably. In three select flowering plants - *Leonotis nepetifolia*, *Tecoma stans* and *Erythrina stricta*, behavioural data was collected.

Defining a “resource unit”

A single tree/shrub or multiple trees/shrubs that are in contact with each other was treated as a single resource unit. Since some shrubs of *Tecoma stans* and herbs of *Leonotis nepetifolia* was so close to each other, forming a single canopy or bush, it did not make sense to treat them as separate units for a) practical and b) ecological reasons. a) It would have been hard to ascertain which plant’s flowers the sunbirds fed on from a distance and b) sunbirds would be attracted to all the flowers of the canopy rather than a part of the canopy of a single shrub/ herb.

Measuring flower abundance

Number of flowers for each sampling occasion was determined using two methods. First, in field, by manually counting the number of flowers in each whorl or cluster and multiplying it with total number of whorls or clusters in the plant. Second, by taking photographs of the resource unit and using software **ImageJ**, flowers were counted. The second method was used when there was an abundant flush of flowers following a rain and it was hard to visually count them in field. Using cell counter tool, the flowers were counted manually quite similar to the first method. Therefore, there would be no more than minor differences in the results of the two methods and can be treated as same.

3.2.2 Sampling behaviour

I observed sunbirds at identified flowering plants from December 2024 to April using Nikon prostaff P3 10*40 binoculars. Every sampling occasion was for 30 minutes each, during

which I noted the number of visits of all sunbirds, their species and sex. I quantified territorial aggression in terms of events of chase. The chase was also classified as interspecific or intraspecific chase.

Defining a “chase”

Many a times a pair of sunbirds (a female and male of the same species, presumably a breeding pair) visiting a patch would chase each other through the canopy and sometimes a parent would chase a juvenile repeatedly. Neither of which have been counted as territorial chases. After observing many territorial chases, I have defined an event of chase as **“when a sunbird flies towards a visitor sunbird, causing it to fly away and also following it into the air for a couple of meters and returning back to the perch, usually close to where the ‘intruder’ foraged.”**

I have also recorded the number of visits and species level identity of other birds that foraged for nectar. I counted the number of flowers in the resource unit after every sampling occasion or took photos of the plant using Nikon P900.

Determining the “Minimum no. of visitors”

Since all the sunbirds visiting resource are not colour banded, the individual identities of sunbirds couldn't be determined. Hence, the true number of visitors to a resource couldn't be ascertained. Therefore, an indirect measure “Minimum no. of visitors” had to be established as a surrogate for intruder pressure. For example, in a sampling occasion, where there are 10 non- overlapping visits by male purple sunbird and one visit by female purple sunbird, the minimum number of visitors would be two. Though it is absolutely possible that there were 10 different male purple sunbirds or two, finding that out is well beyond the scope of the study.

Since, birds have memory and they repeatedly visit a resource until it is exhausted, it is safe to assume that only one male purple sunbird made repeated visits.

3.2.3 Quantifying nectar characteristics

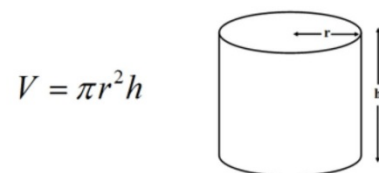
The flowers/inflorescence were bagged in the evening using paper bags made using newspaper and taped to the stalks. The next day morning, the volume and sugar concentration

was measured for each flower. The **volume of nectar** was determined using microcapillary tubes (MCT) and a scale. For the three different flowers, slightly different methods were used to transfer the nectar contents of the flower into the microcapillary tubes.

For *Leonotis nepetifolia*, the verticels were bagged the previous evening using paper bags and the next day morning around 9 am the bags were opened for measuring nectar characteristics. This is done to prevent removal of nectar by visitors. Measurements were not done before 9 am as the flowers secrete nectar all through the night until 8 am. Flowers (n=28) were carefully plucked from the plant and the base of the flower was squeezed into the MCT (Raju & C Reddi, 1994). Then using a millimetre scale ruler, the length (in mm) the nectar had travelled in the MCT was measured.

For *Tecoma stans*, the flower clusters were bagged the previous evening using paper bags and the next day morning around 9 am the bags were opened for measuring nectar characteristics. The base of the flower was crisp and fragile and hence it was not possible to squeeze out the nectar without damaging the flower. Therefore, the inflorescence (n=11) was taken to a lab and using micropipette, the nectar was removed from the base of the flower and then transferred to the MCT. Then, using a millimetre scale, the length (in mm) the nectar had travelled in the MCT was measured.

For *Erythrina stricta*, the flowers stored the nectar between the keel and the standard petals; removing the flower from the pedicel caused spillage of nectar. Hence the same procedure followed for *Tecoma stans* was done using micropipette and MCT. n =14 flowers were measured for nectar characteristics.



www.monstermaths.com/blog/what-is-the-formula-for-the-volume-of-a-cylinder/2/

Once the lengths travelled by nectar was measured for all the flowers, the **volume (mm³)** was calculated using the formula: $v = \pi r^2 h$

r = The internal radius of the MCT = 0.35mm

h = length travelled by nectar in MCT (mm)

The **concentration of the nectar** was measured using an ERMA hand refractometer (0-90%) in field. It measures sugar concentration in percentage brix, which is (g/ml). The instrument was first calibrated to 0% using distilled water. Subsequently, after nectar was removed from the flower for measuring the volume, it was transferred from the MCT to the glass slide of the refractometer and the brix % was read and noted down for every flower.

The amount of sucrose (in g) for every flower was calculated using the formula:

$$\text{Amount of sucrose (g)} = (\text{Concentration (g/ml)/1000}) * \text{Volume (mm}^3\text{)}$$

The mean amount of sucrose per flower was calculated for all three species.

To calculate the **total available sucrose** in a “resource unit” for a given sampling occasion, the aforementioned mean amount of sucrose per flower was multiplied by the **Number of flowers**, respective to the species of the flower.

3.3 Analytical methods

3.3.1 Description of flowering phenologies of sunbird flowers

To depict the dynamics of sunbird resources, a Gantt chart was prepared in RStudio, using the package “tibble”. The flowering periods of all the observed sunbird flowers was depicted in the chart. To depict the change in resource availability with time, the flower abundance was measured every day from the day of identification of the patch till end of flowering period in *Leonotis nepetifolia*.

3.3.2 General summaries of nectar characteristics

To visualise the differences in nectar volume and concentration per flower between the three plant species (i.e., *Leonotis nepetifolia*, *Tecoma stans* and *Erythrina stricta*), box plots were made using excel.

3.3.3 General summaries of sunbird - resource interactions

To visualize the differences in visits, visitation rate, rate of chase and interspecific and intraspecific rate of chase between the three plant species, bar plots were made using excel.

3.3.4 Relationships between flower abundance and visitation by sunbirds

Linear models were used to build regressions between the visits of sunbirds versus resource abundance for all plants and for the three species of plants individually. When all plants were treated equally, the flower abundance was multiplied with the respective average sucrose per flower to get total available sucrose per sampling occasion. This variable was used as independent variable to see the effect in number of visits.

3.3.5 Territorial behaviour in all plants

Quadratic models were used to look at the effect of flower abundance and total sucrose on events of chase for all plants. A bar graph was made to visualize the effect of intruder pressure on territoriality.

3.3.5 Territorial behaviour in *Tecoma stans*

Quadratic models were used to look at the effect of flower abundance on events of chase for *Tecoma stans*. The same was also used to look at the effect of intruder pressure on events of chase in *Tecoma stans*. Partial correlation was done to find the relationships between flower abundance and visitation by sunbirds when controlled for chases in *Tecoma stans*.

3.3.6 Territorial behaviour in *Erythrina stricta*

Partial correlation was done to find the relationships between flower abundance and visitation by sunbirds when controlled for visitation by bigger bodied birds in *Erythrina stricta*. Linear modelling was done to find the effect of bigger bodied birds on the visitation by sunbirds.

4. Results

4.1 Summary of sunbird flowers

A total of 8 flowering plants were identified as sunbird flowers of which only *Tecoma stans* flowered all through the study period. All herbs ceased flowering by end of January. In the spring of 2025, in march, many trees and shrubs flowered of which only *Erythrina stricta* was used by sunbirds as a nectar source.

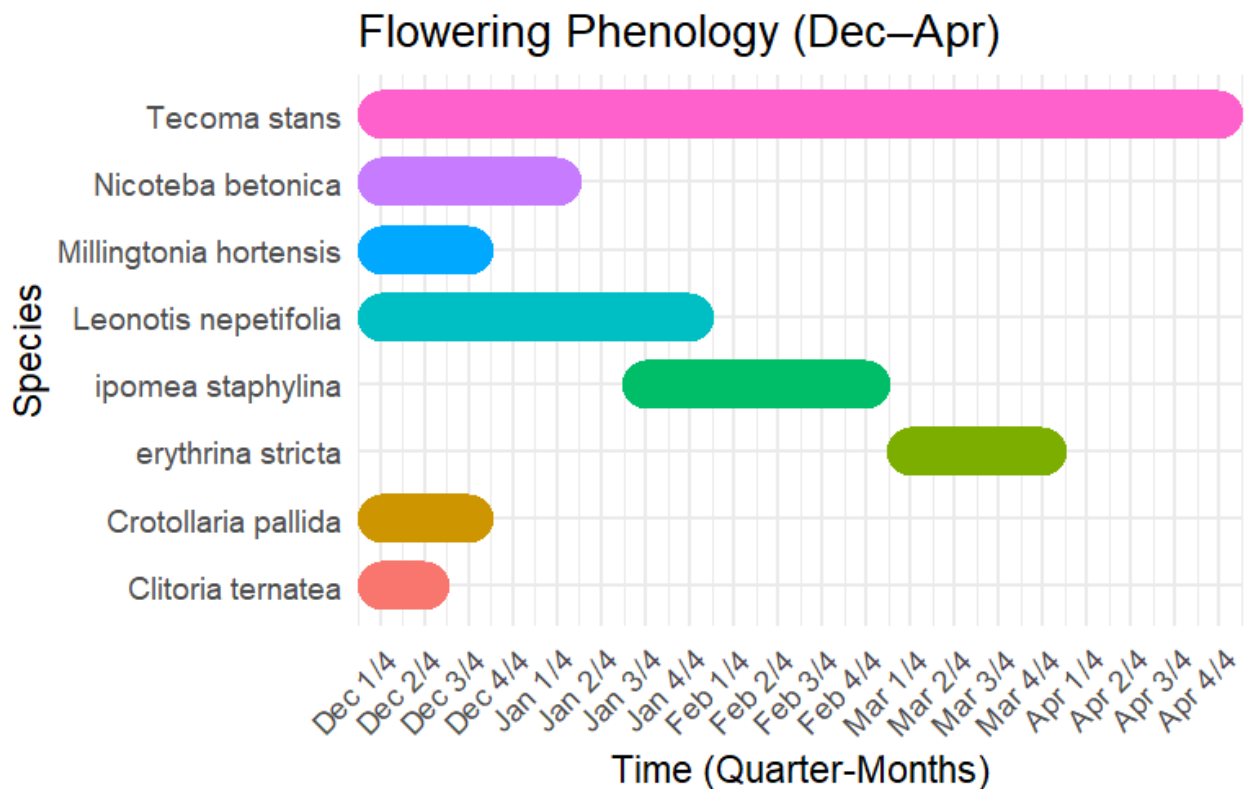


Figure 1: Gantt plot depicting the flowering period of different sunbird flowers

Of the 8 flowering plants that were identified as sunbird flowers, 5 species were native to the Indian subcontinent and 3 were exotic species. I classified sunbird activity in a plant into low, medium and high, based on the average number of visitors for a plant in 30 minutes.

High > 3 visitors, medium \leq 2 visitors, low < 1 visitor

Table 1: Origin, family, habit and sunbird activity of sunbird flowers

S. no	Origin*	Family*	Species	Habit*	sunbird activity
1	exotic	Bignoniaceae	<i>Millingtonia hortensis</i>	Tree	High
2	exotic	Bignoniaceae	<i>Tecoma stans</i>	Shrub	High
3	native	Lamiaceae	<i>Leonotis nepetifolia</i>	Subshrub	Medium
4	native	Fabaceae	<i>Crotolaria pallida</i>	Subshrub	Low
5	native	Acanthaceae	<i>Nicotaba betonica</i>	Subshrub	Low
6	exotic	Fabaceae	<i>Clitoria ternatea</i>	Subshrub	Low
7	native	Convolvulaceae	<i>Ipomea staphylina</i>	Climber	Low
8	native	Fabaceae	<i>Erythrina stricta</i>	Tree	High
9	native	Cornaceae	<i>Alangium salviifolium</i>	Tree	High

*Origin, family, and habit was referred from the website of Royal Botanical Garden, Kew.

(www.powo.science.kew.org)

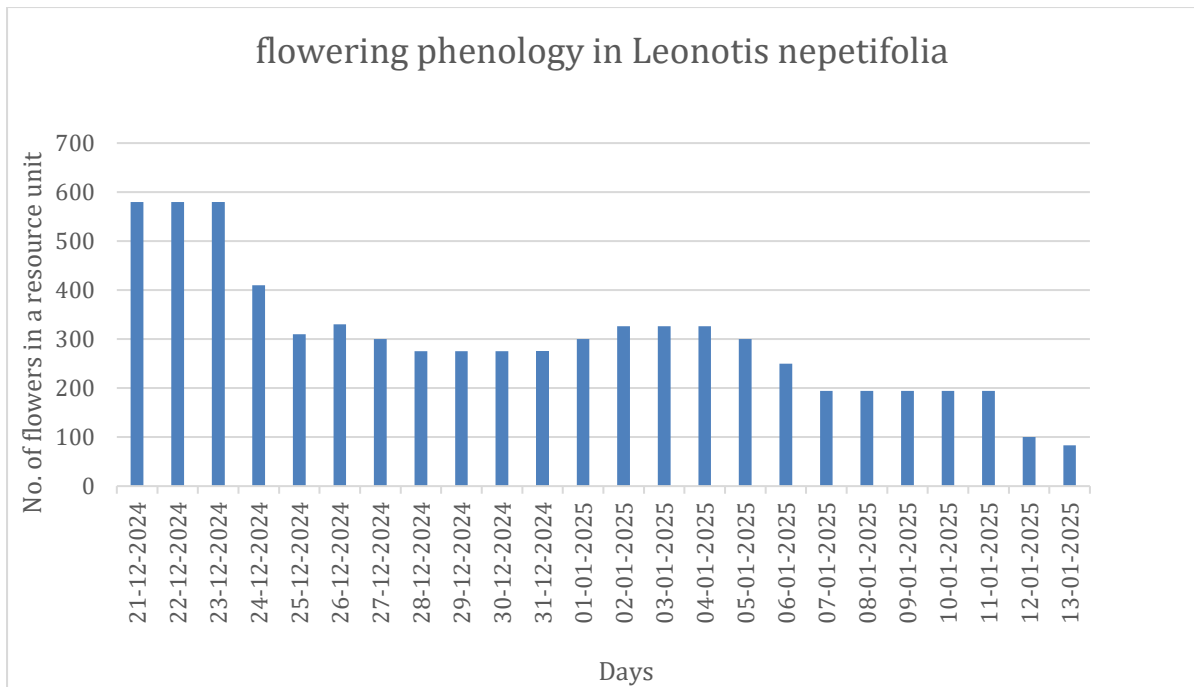


Figure 2. Bar plot depicting flowering phenology in *Leonotis nepetifolia*

The flower abundance of *Leonotis nepetifolia*, i.e., the number of flowers in one resource unit (a patch 40-50 plants present in close proximity to one another), steadily dropped from the end of December 2024 until mid of January 2025, when it completely ceased flowering.

4.2 General summaries of nectar characteristics

Tecoma stans has the highest **mean nectar concentration per flower \pm SD** of 23.52 ± 3.97 % (n=11) followed by *Leonotis nepetifolia*, 16.52 ± 0.72 % (n=28) and *Erythrina stricta* 7.69 ± 0.61 % (n=14) had the least nectar concentration.

The mean nectar volumes of the flowers follow a reverse pattern compared to that of concentration. The **mean nectar volume per flower \pm SD** for the plants are as follows. *Erythrina stricta* $26.65 \pm 11.2\mu\text{L}$, *Leonotis nepetifolia* $9.12 \pm 2.9 \mu\text{L}$, *Tecoma stans* $0.88 \pm 0.76\mu\text{L}$.

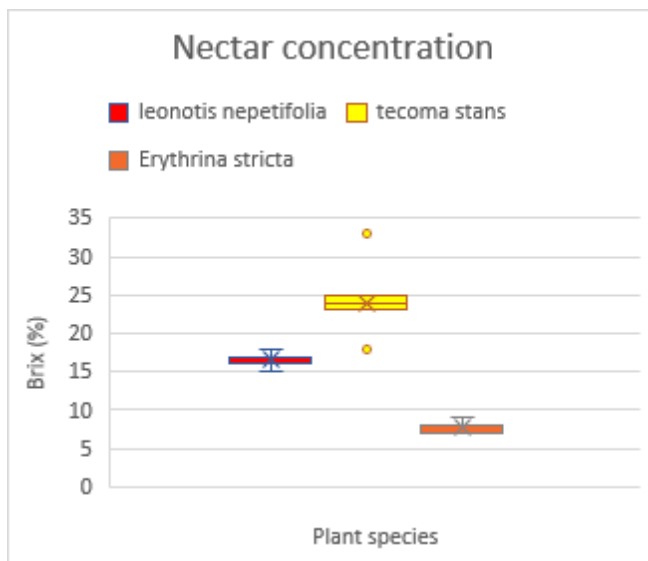


Figure 3. Box plot depicting the nectar concentration per flower of each plant species

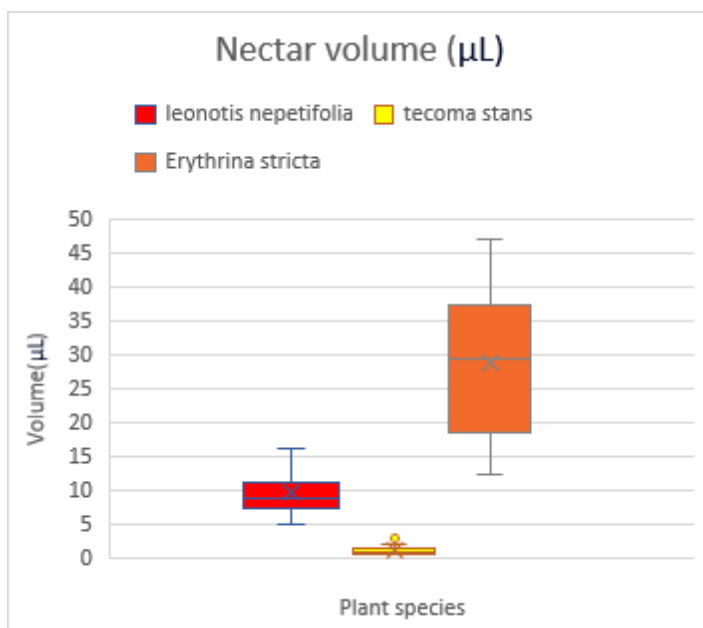


Figure 4. Box plot depicting the nectar volume per flower of each plant species

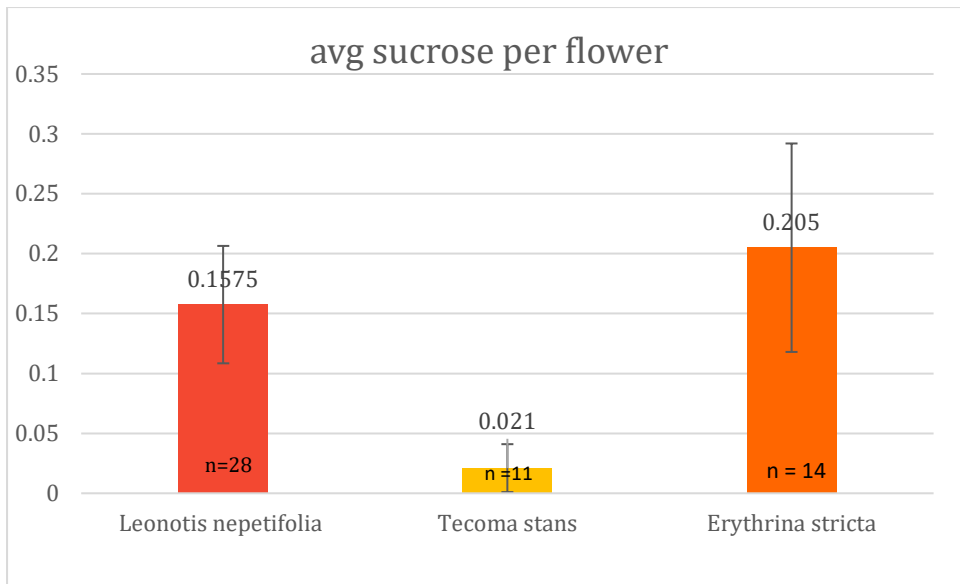


Figure 5. Box plot depicting the average sucrose per flower of each plant species

4.3 General summaries of sunbird - resource interactions

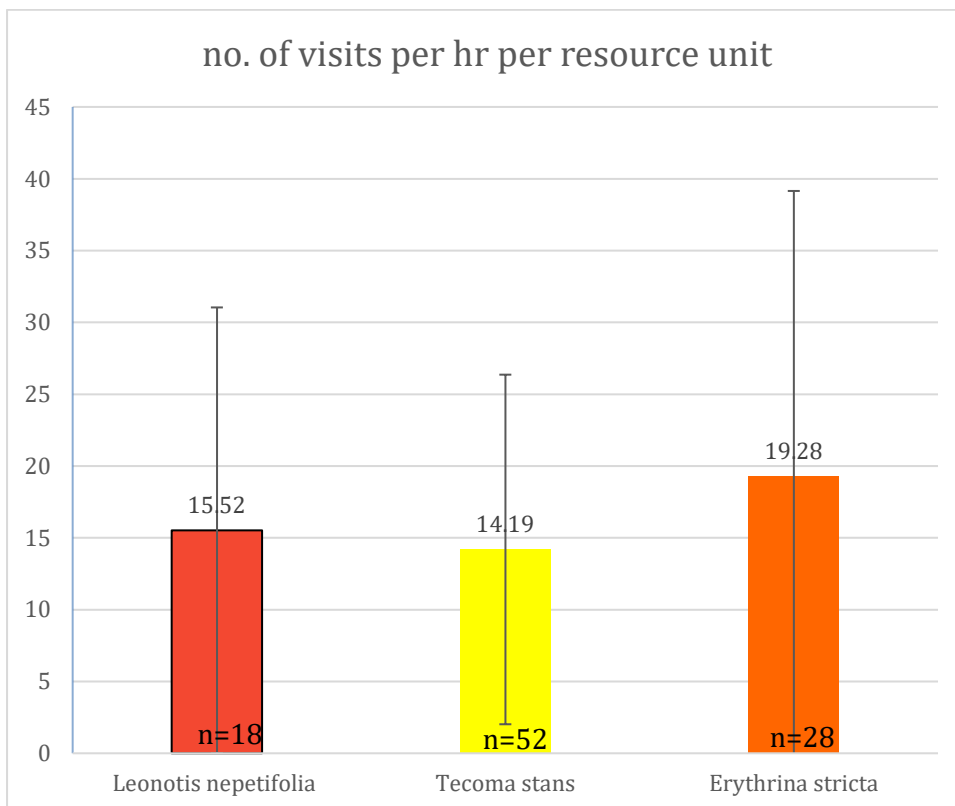
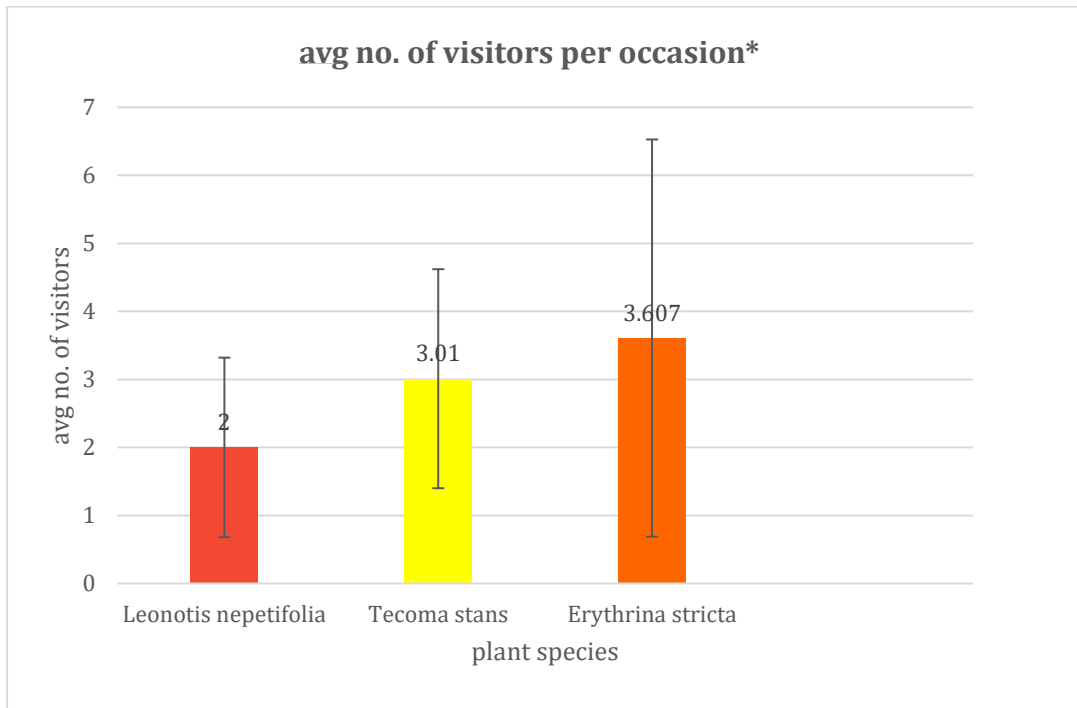


Figure 6. Bar plot depicting the visitation rate in each plant species



*occasion = 30 mins

Figure 7. Bar plot depicting the average number of visitors per occasion in each plant species

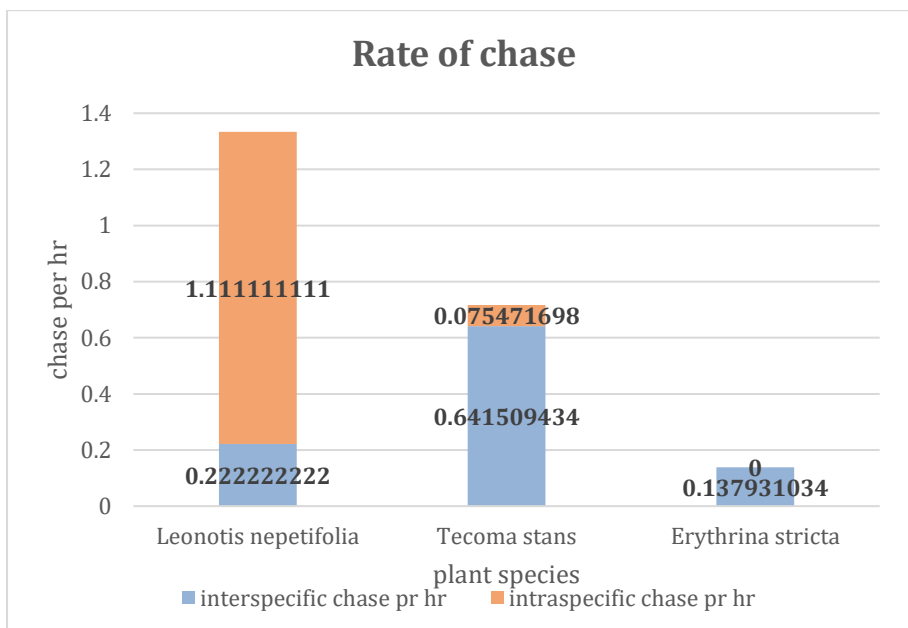


Figure 8. Stacked column bar plot depicting the interspecific and intraspecific rate of chase in each plant species

4.4 Relationships between flower abundance and visitation by sunbirds

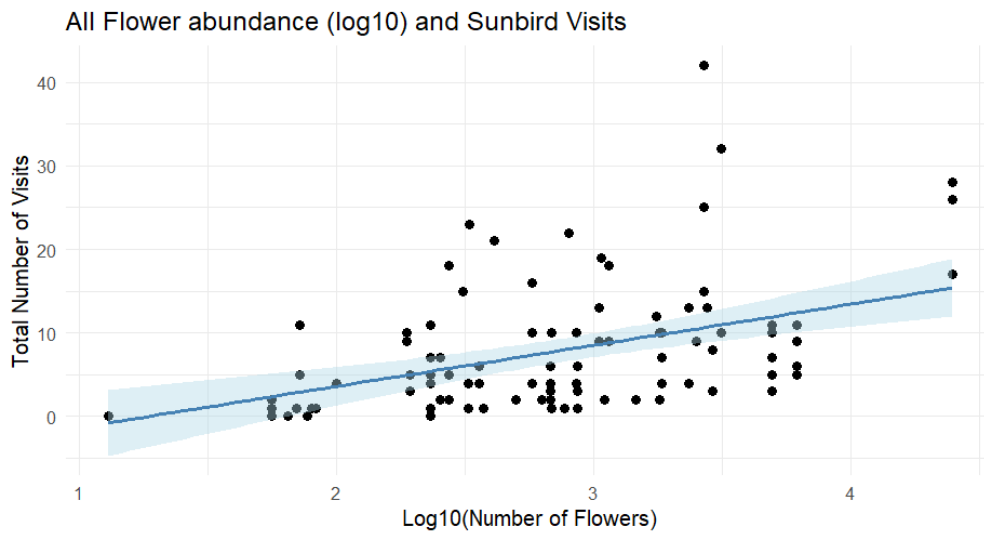


Figure 9. Linear regression depicting the relationship between total number of visits and log₁₀ (no. of flowers) for all three plants

The flower abundance of all plants had a significant effect on the Total number of visits, though the fit was very weak; the model only explained 18% of the variance.

Table 3. Summary of linear model of total number of visits against log₁₀ (no. of flowers) for all three plants

lm(formula = total_no_of_visits ~ log_no_of_flowers, data = filtered_data)					
	Estimate	Std. error	t value	p value	R ²
Intercept	-6.24	3.12	-1.99	0.04*	0.18
Log_no_of_flowers	4.91	1.05	4.66	<0.0001***	

*Significant at 5%

***Significant at 0.01%

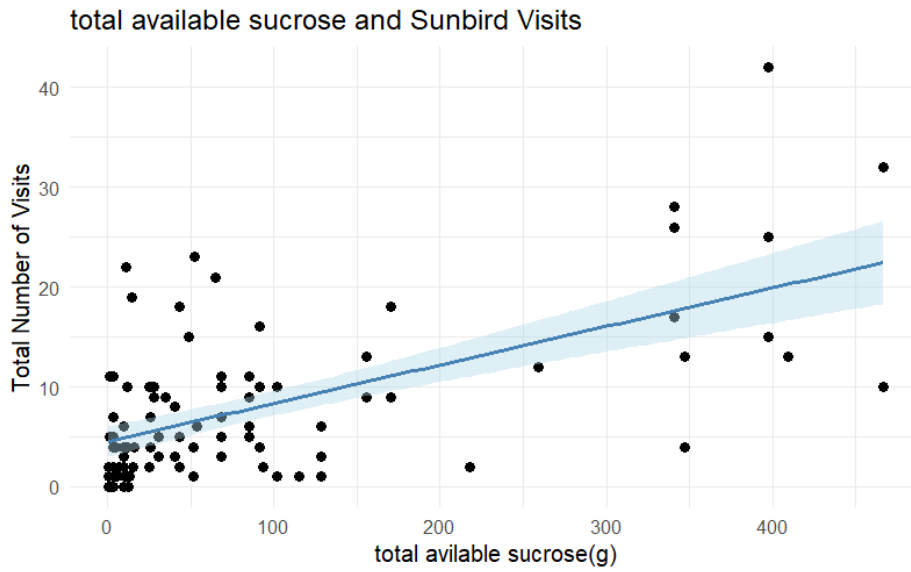


Figure 10. Linear regression depicting the relationship between total number of visits and total available sucrose for all three plants

The total available sucrose of all plants had a significant effect on the Total number of visits and the fit was stronger; the model explained 35% of the variance.

Table 4. Summary of linear model of total number of visits against total available sucrose for all three plants

lm(formula = total_no_of_visits ~ total_available_sucrose, data = filtered_data)					
	Estimate	Std. error	t value	p value	R ²
Intercept	4.51	0.78	5.75	<0.0001***	0.35
total_available_sucrose	0.03	0.005	7.26	<0.0001***	

***Significant at 0.01%

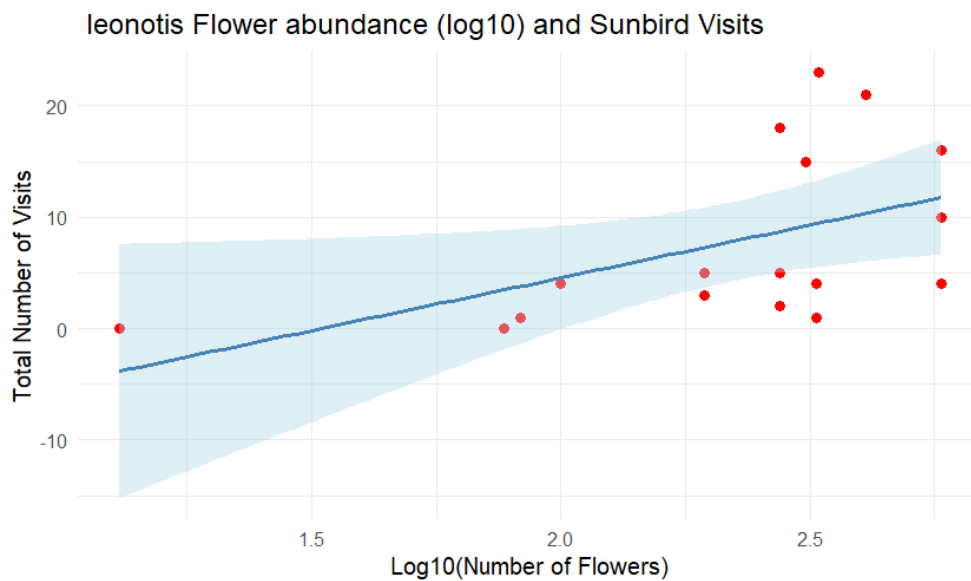


Figure 11. Linear regression depicting the relationship between total number of visits and log₁₀ (no. of flowers) for *Leonotis nepetifolia*

log₁₀(no. of flowers) for *Leonotis nepetifolia* had a significant effect on the sunbird visitation and the model explained 25% of data.

Table 5. Summary of linear model of total number of visits against log₁₀(no. of flowers) for *Leonotis nepetifolia*

lm(formula = total_no_of_visits ~ log_no_of_flowers, data = leonotis_data)					
	Estimate	Std. error	t value	p value	R ²
Intercept	-14.37	9.85	-1.45	0.16	0.25
log_no_of_flowers	9.47	4.15	2.28	0.03*	

*Significant at 5%

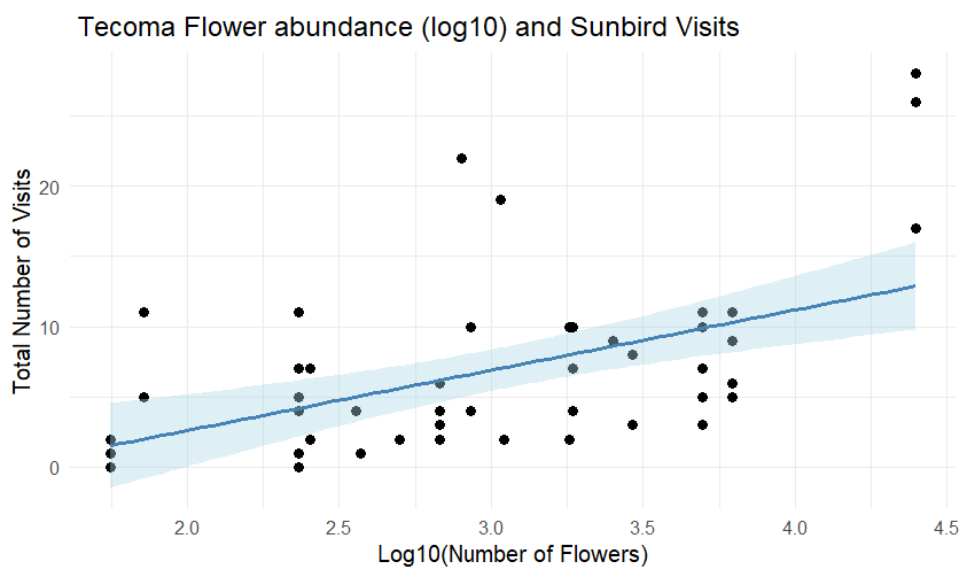


Figure 12. Linear regression depicting the relationship between total number of visits and log10 (no. of flowers) for *Tecoma stans*

log10 (no. of flowers) for *Tecoma stans* had a significant effect on the sunbird visitation and the model explained 26% of data.

Table 6. Summary of linear model of total number of visits against log10(no. of flowers) for *Tecoma stans*

lm(formula = total_no_of_visits ~ log_no_of_flowers, data = tecoma_data)					
	Estimate	Std. error	t value	p value	R ²
Intercept	-5.94	3.14	-1.88	0.06	0.26
log_no_of_flowers	4.28	1.005	4.25	<0.0001***	

***Significant at 0.01%

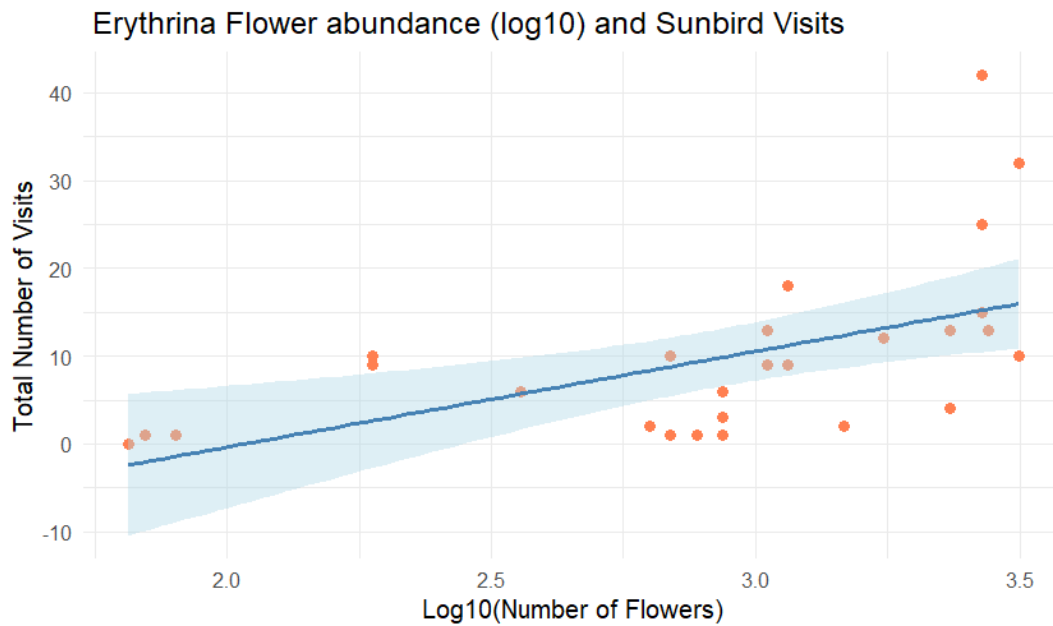


Figure 13. Linear regression depicting the relationship between total number of visits and log10 (no. of flowers) for *Erythrina stricta*

In the fifth case, log10(no. of flowers) for *Erythrina stricta* had a significant effect (p-value =0.002) on the sunbird visitation and the model explained 30% of data.

Table 7. Summary of linear model of total number of visits against log10(no. of flowers) for *Erythrina stricta*

lm(formula = total_no_of_visits ~ log_no_of_flowers, data = erythrina_data)					
	Estimate	Std. error	t value	p value	R ²
Intercept	-22.15	9.62	-2.30	0.02*	0.30
log_no_of_flowers	10.90	3.25	3.35	0.002**	

*Significant at 5%

**Significant at 1%

4.5 Territorial behaviour in all plants

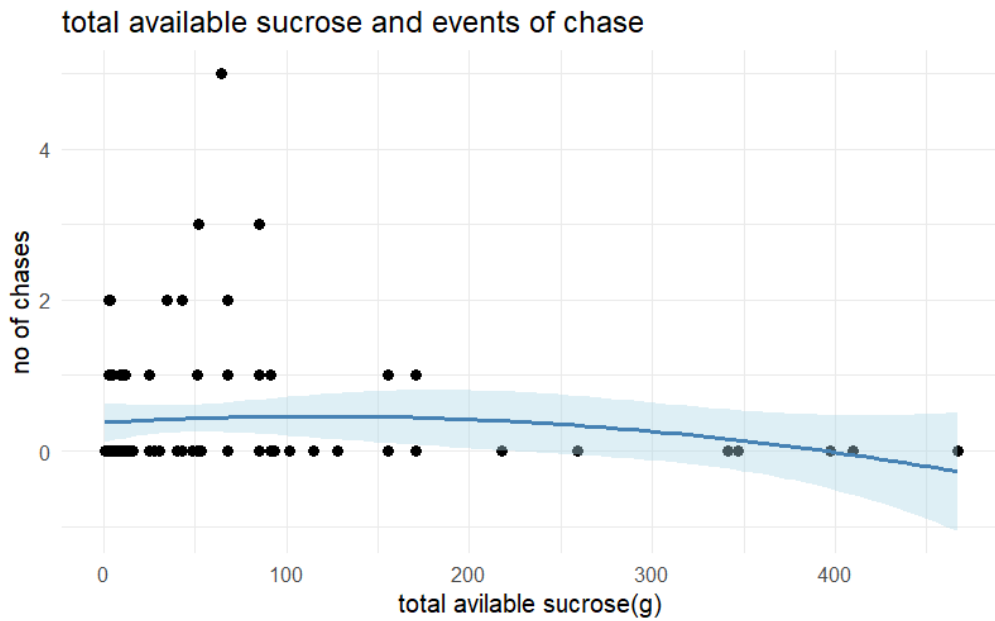


Figure 14. Quadratic regression depicting the relationship between total available sucrose and events of chase for all plants

Table 8. Summary of the quadratic model of total events of chase against total available sucrose for all plants

lm(formula = total_events_of_chase ~ total_sucrose + I(total_sucrose^2))					
	Estimate	Std. error	t value	p value	R ²
Intercept	0.37	0.13	2.87	0.005**	0.03
total_sucrose	0.0014	0.002	0.56	0.57	
I(total_sucrose^2)	-6×10^{-6}	6.03×10^{-6}	-0.99	0.32	

**Significant at 1%

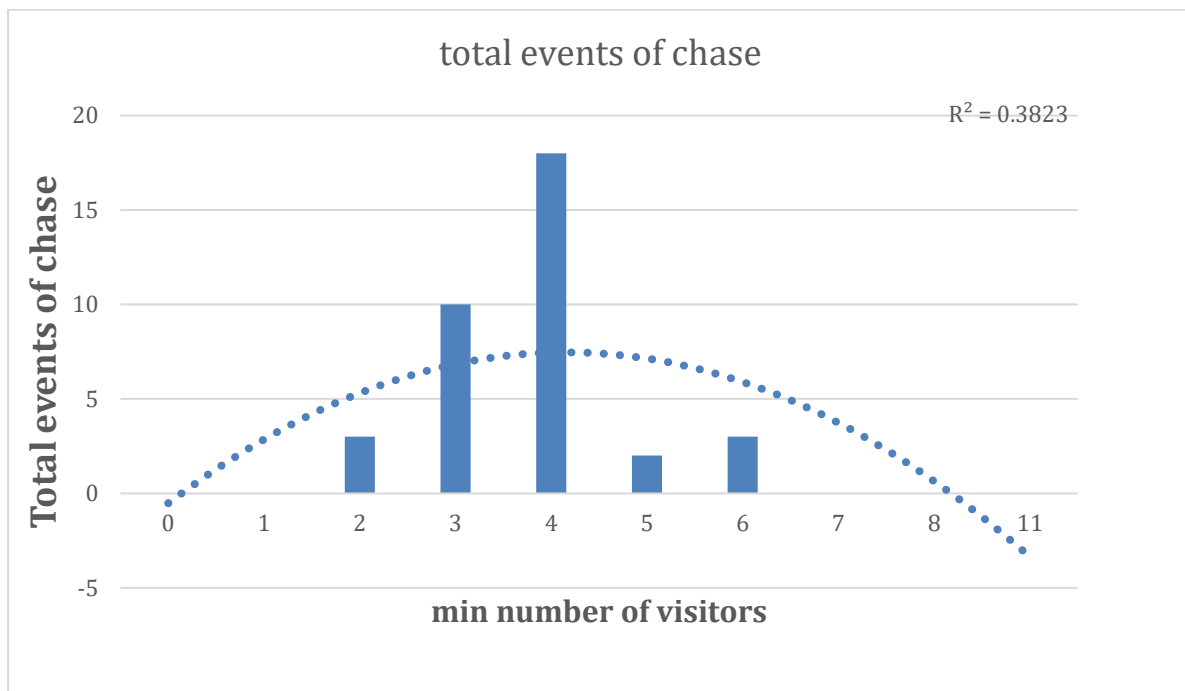


Figure 15. Bar plot depicting the total events of chase recorded at every value of visitor in all plants

This figure is representative of how the aggression is a quadratic function of intruder pressure (Lederer, 1981). The presence of a threshold/peak value of intruder pressure, up until which aggression increases after which, it decreases suggests that sunbird territorial behaviour could be a function of intruder pressure or as a response to intruder pressure. In the subsequent sections it is handled in detail in *Tecoma stans*.

4.6 Territorial behaviour in *Tecoma stans*

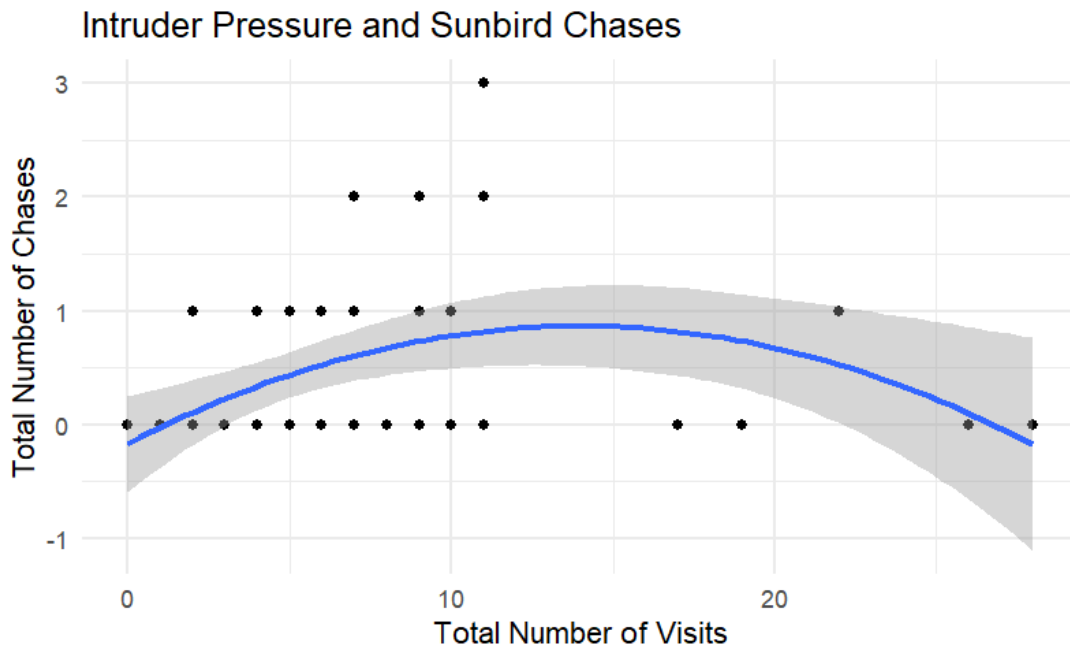


Figure 16. Quadratic regression depicting the relationship between number of chases and total number of visits for *Tecoma stans*

The linear model summary shows a quadratic relationship between the **total number of visits** and the **total events of chase**.

Table 9. Summary of quadratic model of total number of chases against total number of visits for *Tecoma stans*

lm(formula = total_events_of_chase ~ total_no_of_visits + I(total_no_of_visits^2))					
	Estimate	Std. error	t value	p value	R ²
Intercept	-0.16	0.2	-0.8	0.42	0.17
total_no_of_visits	0.14	0.04	3.25	0.002**	
I(total_no_of_visits^2)	-0.005	0.001	-3.03	0.003**	

**Significant at 1%

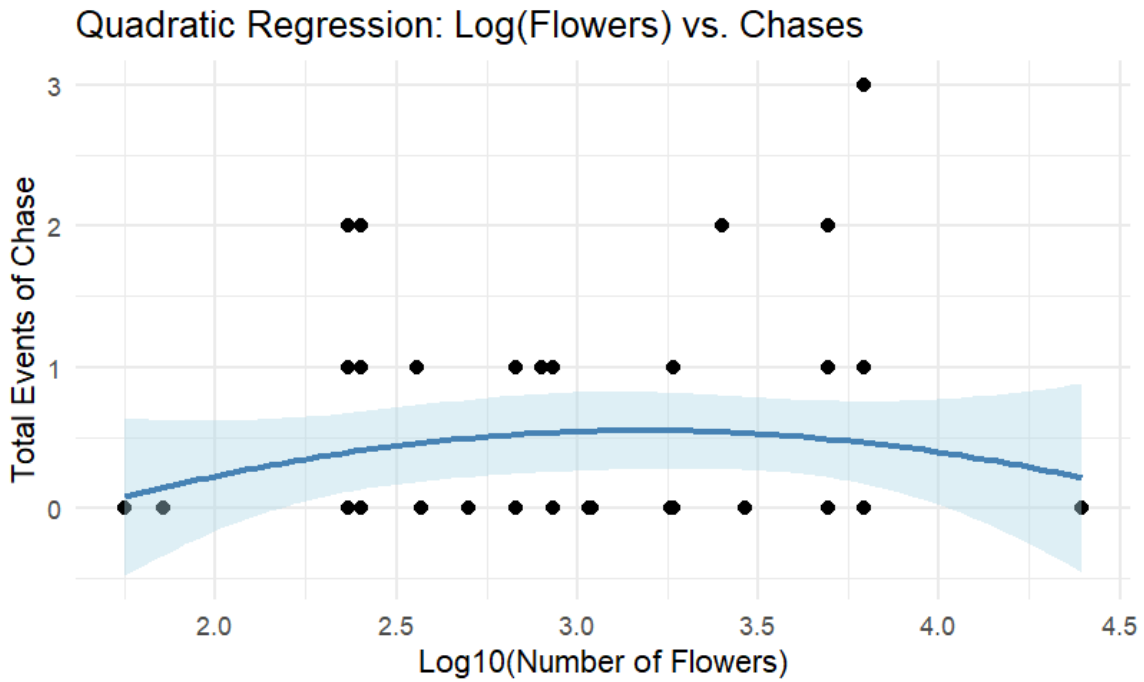


Figure 17. Quadratic regression depicting the relationship between number of chases and log10 (number of flowers) for *Tecoma stans*

Table 10. Summary of quadratic model of total number of chases against log10 (number of flowers) for *Tecoma stans*

lm(formula = total_events_of_chase ~ log_no_of_flowers + I(log_no_of_flowers^2))					
	Estimate	Std. error	t value	p value	R ²
Intercept	-1.77	1.58	-1.11	0.27	0.03
log_no_of_flowers	1.45	1.09	1.33	0.18	
I(log_no_of_flowers^2)	-0.22	0.18	-1.26	0.21	

4.7 Territorial behaviour in *Erythrina stricta*

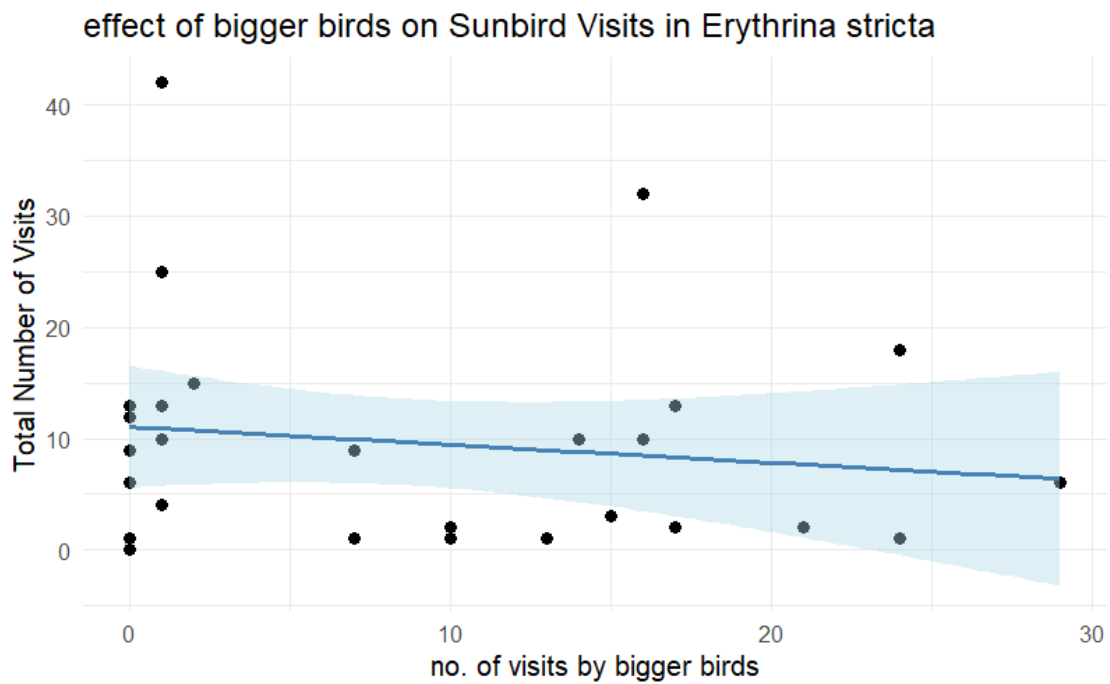


Figure 18. Linear regression depicting the relationship between total no. of visits of sunbirds and no. of visits of bigger bodied birds

Table 11. Summary of linear model of total number of sunbird visits and no. of visits of bigger bodied birds in *Erythrina stricta*

lm(formula = total_no_of_visits ~ no_of_other_bird_visits, data = erythrina_data)					
	Estimate	Std. error	t value	p value	R ²
Intercept	11.06	2.65	4.16	<0.001***	0.02
no_of_other_bird_visits	-0.16	0.21	-0.76	0.45	

***Significant at 0.1%

Added-Variable Plots

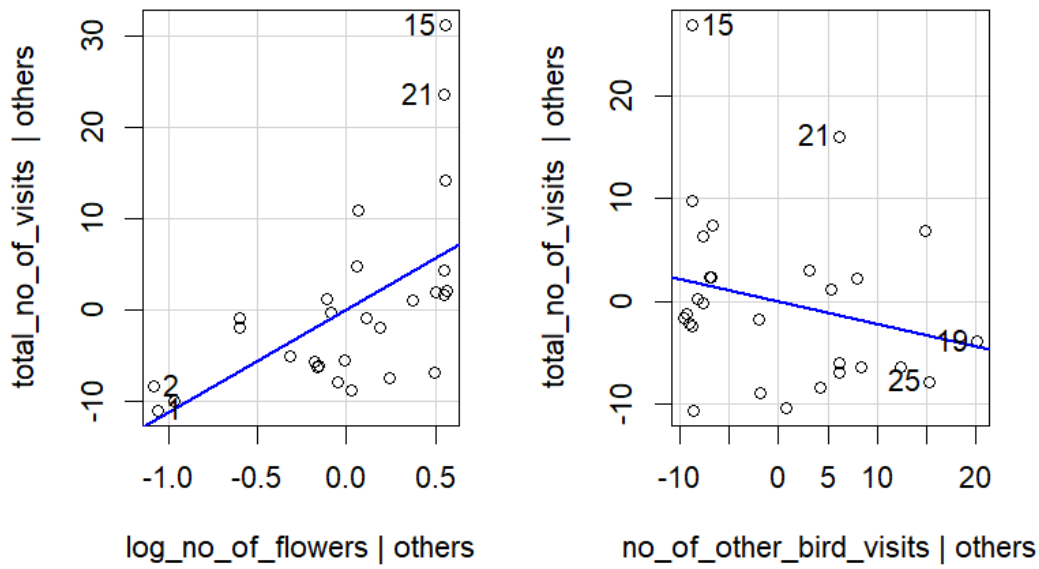


Figure 19. Partial correlation between total number of visits and log₁₀ (no. of flowers) controlled for number of visits of bigger bodied birds in *Erythrina stricta*

Table 12. Summary of partial correlation of total number of sunbird visits and no. of visits of bigger bodied birds in *Erythrina stricta*

	log_no_of_flowers	total_no_of_visits	no_of_other_bird_visits
log_no_of_flowers	0.000000000	0.001807872	0.2817359
total_no_of_visits	0.001807872	0.000000000	0.2255647
no_of_other_bird_visits	0.2817359	0.2255647	0.000000000

When controlled for no. of the other bird visits, flower abundance has a significant effect on sunbird visits (p-value = **0.0018**)

5. Discussion

5.1 Summary of sunbird flowers

Within a couple of weeks of spending time in the scrub jungle of Anaikatti hills, I found that determining a sunbird flower was more challenging than I had anticipated. Firstly, When a sunbird was found foraging on a flower, it was presumptuous to assume that they were feeding on nectar. They could perhaps be foraging for spiders or even drinking mist collected at the base of the flower. This was dealt cautiously, as noted by Dr. Salim Ali in his paper “Flower-birds and bird-flowers in India” and only flowers that had predictable and repeated visits were considered as sunbird flowers in this study. Secondly, more often than not sunbirds were found in plants/trees with no flowers. Though, it is a known fact that sunbirds are also insectivorous (Ali, S. 2002), the extent to which they were, was quite surprising, and if I may say so quite frustrating. Especially during the dry period from the last week of January 2025 to second week of February 2025, there were no flowers, let alone sunbird-flowers, except for the flowers of the planted avenue trees of *Tecoma stans*.

Millingtonia hortensis, a member of the family Bignoniaceae, was in bloom at the time of my arrival at the study site during the first week of December 2024. The flowers are white, elongated and bell shaped. The calyx is a slender, long tube that divides into four petals (R.Ramasubramaniam, 2010). It attracted a lot of sunbird visitors, especially, purple and purple rumped sunbird. The sunbirds were often found hovering near the flower’s mouth, and sometimes they were also found nectar robbing by piercing the base of the flower. It is possibly because they weren’t able to reach the deeply seated nectaries of the flower, as the calyx is narrow and longer than their bill lengths (Irwin et al., 2010).

Since, the trees ceased flowering before the initial survey period, behavioural data of sunbirds couldn’t be collected.

Crotolaria pallida, a member of the family Fabaceae, had yellow tubular flowers with red veins that attracted purple rumped sunbirds, though in very low numbers. The population of the plant was too low to collect behavioural data.

Nicotiana glauca, a member of family Solanaceae, was found along streams. It had tiny white flowers that had nectar at the base, which attracted sunbirds occasionally.

Clitoria ternatea, again, a member of the family Fabaceae, boasted bright bluish-purple flowers, that again, only occasionally attracted sunbirds. And the plant population was too low in the campus.

Ipomea stacylina, a member of the family Convolvulaceae with pinkish purple flowers, occasionally had sunbird visitors. All attempts to draw nectar out of this flower was futile. Because of such a low nectar quantity, sunbirds might not have been attracted to it despite it blooming in large numbers during February.

The summaries of *Leonotis nepetifolia*, *Tecoma stans* and *Erythrina stricta* will be discussed in subsequent sections.

5.2 General summaries of nectar characteristics

Leonotis nepetifolia, is suggested to be a typical sunbird pollinated flower (Gill & Wolf, 1975). The bright orangish-red and tubular corolla, as well the absence of lower lip and presence of perches, all indicate a sunbird-pollination syndrome. It has an average nectar concentration ($\bar{x} = 16.52$, $SD = 0.72$) %, ($n=28$) and average nectar volume ($\bar{x} = 9.12$, $SD = 2.9$) μL , ($n=28$), which is considered to be quite dilute and voluminous as compared to insect pollinated flowers. Using these values, the average sucrose present per flower is calculated to be ($\bar{x} = 0.150$, $SD = 0.049$) g.

Tecoma stans, is suggested to be a typical hymenopteran pollinated flower (Curti & Ortega-Baes, 2011) in its native range in Central America. The sunbirds in the study area, mostly robbed nectar by piercing the base of the flower. It is worthy to note here that, the floral architecture majorly determines the foraging tactics of the pollinator (Janeček et al., 2011; Rojas-Nossa et al., 2016). *Tecoma stans* had high nectar concentration ($\bar{x} = 23.52$, $SD = 3.97$) %, ($n=11$) and low nectar volume ($\bar{x} = 0.88$, $SD = 0.76$) μL , ($n=11$) as expected for an insect-flower. The average sucrose present per flower is calculated to be ($\bar{x} = 0.020$, $SD = 0.02$) g.

Erythrina stricta, is considered to be a typical bird flower. The tree is deciduous, shedding all its leaves during winter. During spring, the tree is fully naked but for bright coral red flowers.

The nectar is collected between the standard and the keel petals. In fact, the entire genus of *Erythrina* is mostly bird pollinated (Hemsley & Ferguson, 1985; Neill, 1987; Raven, 1979). The bright red flowers of *Erythrina stricta* have copious amounts ($\bar{x} = 26.65$, $SD = 11.2$) μL , ($n=14$) of very dilute nectar ($\bar{x} = 7.69$, $SD = 0.61$) %, ($n=14$), and attract many bigger bodied bird visitors like White bellied Drongo, Red-vented bulbuls, Orioles, etc (refer appendix) other than sunbirds. Of all the birds that visited the flowers, ($n=26$) only two birds were non-Passeriformes.

The average sucrose present per flower is calculated to be ($\bar{x} = 0.205$, $SD = 0.087$) g. **It is worthy to note here that though *Leonotis nepetifolia* and *Erythrina stricta* have very different nectar concentration and volume, the calculated sugar per flower is quite close.**

5.3 General summaries of sunbird - resource interactions

Visitation rate

Erythrina stricta has the highest visitation rate among the three species – 19.28 visits per hr. this could be because of the richness of the resource, as it has the highest average sucrose per flower ($\bar{x} = 0.205$, $SD = 0.087$) g.

Leonotis nepetifolia and *Tecoma stans* with 15.5 visits per hr and 14.19 visits per hr had lower visitation rate compared to *Erythrina stricta*. *Tecoma stans* was a vegetatively complex resource unit with branches, that allowed for sunbirds to stay in the resource unit for longer, which reflected in the lower visitation rate. And in *Leonotis nepetifolia*, data was collected in one resource unit on multiple days, to see the change in their behaviour with changing flower abundance. the entire resource unit was defended by a pair of purple sunbirds and they were fiercely defending the resource unit, and made frequent visits.

Rate of chase

Among the three sunbird flowers, *Leonotis nepetifolia* has the highest intraspecific chase of 1.1 chase per hr. this can be attributed to the fact that it was fiercely defended by a pair of sunbirds from other purple sunbirds.

Tecoma stans has the highest interspecific chase as, all three sunbirds were attracted to the flowers, and all of them faced aggression.

Erythrina stricta has the lowest rate of chase, as sunbirds found it hard to even forage for nectar as they were constantly bullied and chased away by the bigger birds. They had to be smart to just to forage for nectar, leaving no space for aggression among sunbirds both inter and intra specifically. Sunbirds were attracted in large numbers, yet little aggression was observed.

5.4 Relationships between flower abundance and visitation by sunbirds

During the early evolution of flowering plants, they struck jackpot in using insects for their reproductive endeavours. Over many millennia, plants and insects co-evolved to exploit each other effectively, giving rise to some of the most fascinating plant-pollinator interactions.

The floral morphology, architecture together with nectar characteristics decide which pollinators are appreciated at a flower and who are not (Cronk & Ojeda, 2008).

I analysed the effect of floral abundance on the visits of sunbirds in 5 ways. In the first case, I treated all three plants (*Leonotis nepetifolia*, *Erythrina stricta* and *Tecoma stans*) as equal, assuming the floral architecture and nectar characteristics don't affect the sunbird visitation. I regressed the total number of visits against $\log_{10}(\text{no. of flowers})$ for all three plants and found that it had a significant effect ($p\text{-value} = <0.0001$) but the model only explained 18% of the variance. Though, it is intuitive to assume that, number of visits to a resource will increase, with increase in floral abundance, many factors influence this relationship. Perhaps, the presence of a territorial individual might discourage sunbird visits in spite of the presence of high floral abundance as in the case with *Leonotis nepetifolia*. Or, it could be the presence of other bigger bodied birds that deters sunbirds as in the case of *Erythrina stricta*. Also, it is possible, that the floral architecture might demand higher handling time.

In the second case, I multiplied floral abundance with their respective sucrose per flower, to look at their effect on sunbird visitation. I regressed total number of visits against total available sucrose for all three plants and found out that it had a higher significant effect (p-value <0.0001) and higher fit ($r^2=0.35$), almost twice the fit as that of the previous model. This shows the importance of sucrose over just floral abundance to the sunbirds.

The next three models, I regressed total number of visits against floral abundance for each of the three species separately as this made more ecological sense.

In the third case, \log_{10} (no. of flowers) for *Leonotis nepetifolia* had a significant effect (p-value = 0.03) on the sunbird visitation and the model explained 25% of data. The slightly high p value can be attributed to the small sample size of *Leonotis nepetifolia*.

In the fourth case, \log_{10} (no. of flowers) for *Tecoma stans* had a significant effect (p-value <0.0001) on the sunbird visitation and the model explained 26% of data.

In the fifth case, \log_{10} (no. of flowers) for *Erythrina stricta* had a significant effect (p-value =0.002) on the sunbird visitation and the model explained 30% of data. The slightly high p value can be attributed to the small sample size of *Erythrina stricta*.

5.5 Territorial behaviour in all plants

I used the quadratic model to see the effect on the number of chases against total available sucrose. The effect was not significant. It can be inferred that sunbird territorial behaviour is not a function of sucrose amount alone. The breeding state of the sunbirds could be factor affecting territoriality. The non-uniformity of resources, the highly heterogenous vegetation, lack of concentrated resources at a landscape level, could all contribute to the result. As discussed earlier, the sunbirds respond to many other factors that this study couldn't have quantified. It could also be because, in the study period I wasn't able to find as many territorial individuals. Most of the data that I collected is taken from *Tecoma stans*, where sunbirds are known to aggregate without much aggression. This could be because of the super abundant nature of *Tecoma* flowering and the complex vegetation structure of the shrub that makes it difficult to sight and chase away intruders. The figure 17. is representative of how aggression is a quadratic function of intruder pressure (Lederer, 1981). The presence of a peak value of intruder pressure, up until which aggression increases after which, it

decreases suggests that sunbird territorial behaviour could be a function of intruder pressure or as a response to intruder pressure.

5.6 Territorial behaviour in *Tecoma stans*

This section we explore the effect of two major variables on the territorial behaviour of sunbirds in *Tecoma stans*.

- i. Intruder pressure
- ii. Flower abundance

Effect of Intruder pressure:

The **total events of chase** which is a surrogate for territorial aggression, is a quadratic function of **total number of visits**, which is a surrogate for intruder pressure.

The Linear term (total no. of visits) has a positive coefficient (0.14) that suggests that as visits increase, chases increase, up to a threshold point. The Quadratic term (total no. of visits)² has a negative coefficient (-0.005) suggesting the relationship is concave (i.e., inverted- U). After a certain threshold of visits, the number of chases begins to decline. Both predictors are highly significant ($p < 0.01$), implying a strong statistical relationship.

The fit of the model is low, at $r^2 = 17\%$, possibly because of the zero inflated dataset.

Effect of flower abundance:

None of the predictors were found to be statistically significant. Though, the **negative quadratic term** (-0.22) suggests a possible inverted-U relationship, it is not statistically significant. It is also possible that *Tecoma stans* resource units was too rich a foraging area for territorial behaviour, meaning the entirety of flower abundance measured in the study period was above the “hypothetical threshold value for flower abundance”, resulting in this insignificant relationship.

5.7 Territorial behaviour in *Erythrina stricta*

Erythrina stricta was an interesting case of interspecific competition, because sunbirds had to compete with not just congeners and confamilials, but with different families of bigger bodied birds. The relationship between total no. of visits of sunbirds and no. of visits of bigger bodied birds is weakly negatively correlated as the slope for no. of other bird visits is negative (-0.16) even though not statistically significant ($p = 0.45$). this could be because

some erythrina trees that were found in an open area, close to the road, attracted a lot of bigger birds as compared to the erythrina trees that were found in closed canopy areas, slightly deeper in the forest. Despite having similar floral abundances, the bigger bodied birds were found at higher numbers in the open sites and sunbirds were found more in the concealed sites.

A model of partial correlation was run and was found out that, when controlled for no. of the other bird visits, flower abundance has a significant effect on sunbird visits (p-value = **0.0018**) in *Erythrina stricta*.

Natural history notes and going forward...

All through the study period, if there was one persisting question that demanded my attention was the extent of dependence of sunbirds on arthropods. Much to my frustration, there was almost a change in guild, if I may say so, during the dry period of late winter, when almost no sunbird flowers were in bloom. The sunbirds were omnipresent, showing no signs of local movement during that period. On many occasions I observed sunbirds actively gleaning for spiders and arthropod larvae among dried leaves and hovering near spider webs to catch spiders. When new leaves of *Acacia leucophloea* flushed, it was infested with a lepidopteran larva, sunbirds (both purple and purple rumped) flocked at these trees to glean the leaves. They did so effectively by feeding on as many as one in every five seconds. That leads us to the question, what portion of their physiology is actually nectar dependent? How much are they dependent of flowers vs arthropods? And how does that change across seasons?

The other question I had in mind was, what were sunbird flowers? when we imagine sunbird-flower interactions, we have a romanticised view of co-evolution, a flower that is perfectly adapted to manipulate the bird and the bird, perfectly adapted to extract maximum resources from the flower. A simple case of obligatory mutualism. But that is hardly the case. These birds, flowers and this system in extension is more resilient than we know. A complex web of interactions happens in which every species, (both sunbirds and flowers) is dependent on multiple species for their survival. A typical bird flower (bird pollinated flower) is said be bright with conspicuous colours like red, odourless, big, with copious amounts of dilute nectar, all compared to insect flowers.

But sunbirds do not seem to just be attracted to such strong stimulus. They respond to a variety of stimulus. Small inconspicuous, feathery, dull coloured, with very little nectar (less than 1 μ L) producing flowers. What attracts them to a flower? Colour? Shape? Smell? Memory? Calls of other birds? What kind of reward do they feel upon tasting nectar?

And finally, and most importantly, what other factors influence territorial behaviour besides nectar quality, quantity and intruder pressure? It is possible that the distribution of resources in a landscape has an effect? Or the reproductive status perhaps. That leads us to another question, Is the territorial cost equal for all individuals?

Exploring further questions in this system, could help us understand what selection pressures would have selected such flexibility in territorial behaviour in sunbirds and other nectarivores.

6. Conclusion

Sunbird territorial behaviour is a complex response to changing resources and competition. The visitation of sunbirds showed positive correlation and statistical significance to floral abundance. Visitation, which was used as a surrogate for intruder pressure is a significant predictor of territorial behaviour in one plant species. Though flower abundance directly did not predict territorial behaviour, its indirect effect was mediated through intruder pressure in the sunbird community of the study area. Effect of intruder pressure on aggression hinted towards the existence of a threshold model of feeding territoriality. It is worthy to note that the low model fit suggest a much complex system, and feeding territoriality could be dependent on multiple factors other than just nectar availability and competition. There are two caveats to this study; a) The dependence of sunbirds on insects and arachnids was not accounted for, especially in the dry period, it could play a very important role; b) competitors of other taxa was also not included. During the duration of the study, it was observed that competitors to sunbirds, weren't just other sunbirds or other birds, hymenopterans (stingless bees, carpenter bees, ants) and even rodents (three-striped palm squirrels) were found foraging on sunbird-flowers. The effect of landscape level resource density and availability, effect of floral architecture and most importantly the breeding status of sunbirds might all, perhaps play an important role in determining whether a sunbird decides to defend or to not defend.

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Appendix

S. No	Species	Family	Order
1	Ashy Drongo	Dicruridae	Passeriformes
2	Black Hooded Oriole	Oriolidae	Passeriformes
3	Brown Capped Pygmy Woodpecker	Picidae	Piciformes
4	Cinereous Tit	Paridae	Passeriformes
5	Common Babbler	Leiothrichidae	Passeriformes
6	Common Iora	Aegithinidae	Passeriformes
7	Common Myna	Sturnidae	Passeriformes
8	Coppersmith Barbet	Megalaimidae	Piciformes
9	Golden Fronted Leafbird	Chloropseidae	Passeriformes
10	Grey Breasted Prinia	Cisticolidae	Passeriformes
11	Indian Golden Oriole	Oriolidae	Passeriformes
12	Jerdon's Leafbird	Chloropseidae	Passeriformes
13	Jungle Myna	Sturnidae	Passeriformes
14	Malabar Parakeet	Psittaculidae	Psittaciformes
15	Pale Billed Flowerpecker	Dicaeidae	Passeriformes
16	Plum Headed Parakeet	Psittaculidae	Psittaciformes
17	Red Vented Bulbul	Pycnonotidae	Passeriformes
18	Red Whiskered Bulbul	Pycnonotidae	Passeriformes
19	Rufous Treepie	Corvidae	Passeriformes
20	Tailor Bird	Cisticolidae	Passeriformes
21	Warbler sp.	Sylviidae	Passeriformes
22	White Bellied Drongo	Dicruridae	Passeriformes
23	White Browed Bulbul	Pycnonotidae	Passeriformes
24	Yellow Billed Babbler	Leiothrichidae	Passeriformes

